

# NEW PALEOBOTANICAL DATA ON ORIGIN AND EARLY EVOLUTION OF ANGIOSPERMY

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## ABSTRACT

The author's contributions to the problem of angiosperm origin since 1975 are summarized. Jurassic *Hirmerella* is assigned to proangiosperms based on its fruit-like diaspores. Achenes with persistent receptacles bearing long trusses of hairs came from the Lower Cretaceous of Lake Baikal province. They resemble cyperaceous achenes but could have arisen from bennettitalean ovulate receptacles by reduction of ovules to one and fusion of interseminal scales. Angiosperm fruits, grass-like leaves, and several kinds of spikes and spiked heads are found in the Lower Cretaceous of Mongolia. A middle Albian fructification from Kazakhstan with bitegmic ovules is related to Ranunculidae. Some minor findings are mentioned in discussion. The "spotted layer" of *Caytonia* is interpreted as inner integument. Mescogenous stomata and incipient vessel members are revealed in bennettites. Possible links of proangiospermous *Caytonia*, *Dirhopalostachys*, and *Leptostrobus* with angiosperms are indicated.

I have reported on proangiosperms—a rather loose group, comprising *Caytonia*, *Leptostrobus*, and *Dirhopalostachys* which, together with some other plants, such as bennettites, formally not included in the group, provided a "character pool" for arising angiosperms (Krassilov, 1977a). Since then another proangiosperm plant, supposedly of bennettitalean affinity, was found in Baisa, Lake Baikal province. Early Cretaceous angiosperms and angiosperm-like plants were found in Mongolia. Some Albian angiosperm fructifications from Kazakhstan have been re-studied (Vakhrameev & Krassilov, 1979). Some new data on *Hirmerella*, *Caytonia*, and bennettites are also, I believe, relevant to the problem of angiosperm ancestry. These results and their implications are discussed below.

## "OVULIFEROUS SCALES" OF *HIRMERELLA*

This name is applied to ovulate cones of a Jurassic plant that produced pollen grains of *Classopollis* type. *Classopollis* shows some angiosperm-like features (columellate ectexine, striated belt) comparable with equatorial har-momegathus of *Nymphaea*. Ovulate organs of this genus also have angiosperm-like features. *Hirmerella* dispersed rather bulky winged bodies conventionally described as seed scales. However, seeds occurred not on, but within these bodies, which are fruits rather than scales. Harris (1979) found two megaspore membranes within the "scales" and I found two overlapping nucelli in a "scale" from the Lower Jurassic of Poland

(courtesy of Dr. Maria Reymanowna, Krakow and Dr. Maya Doludenko, Moscow).

My interpretation is that there were two ovules per fruit, closely packed and filling a locule. In both British and Polish fruits there were cuticles of the locule adnate to integumental cuticles (Fig. 1). If the ovules were merely embedded in the "scales" there would be no internal cuticle lining the locule.

A lot of pollen grains stick to the papillate surface of the "scales," but none have been observed within the nucelli, which had inconspicuous beaks.

*Hirmerella* radically differs from all known conifers and is perhaps closer to *Ephedra*, which sometimes show two ovules per cupule (Mehra, 1950). Based on its fruit-like diaspores, *Hirmerella* can be included in proangiosperms. It may represent an extinct order of gnetophytes.

## BAISIAN ACHENES

One of the most fascinating discoveries was made recently in the Lake Baikal province. Lower Cretaceous paper shales and marls cropping out along the Vitim River near Baisa camp are well known as the richest Mesozoic locality of terrestrial insects and diverse lacustrine fauna. Fossil plants are less abundant and of trivial Early Cretaceous Siberian aspect (ginkgoaleans, czekanowskias, pinaceous conifers). However, a decade ago paleoentomologists from the Paleontological Institute, Moscow, were lucky to find a single angiosperm-like leaf described by Vakh-

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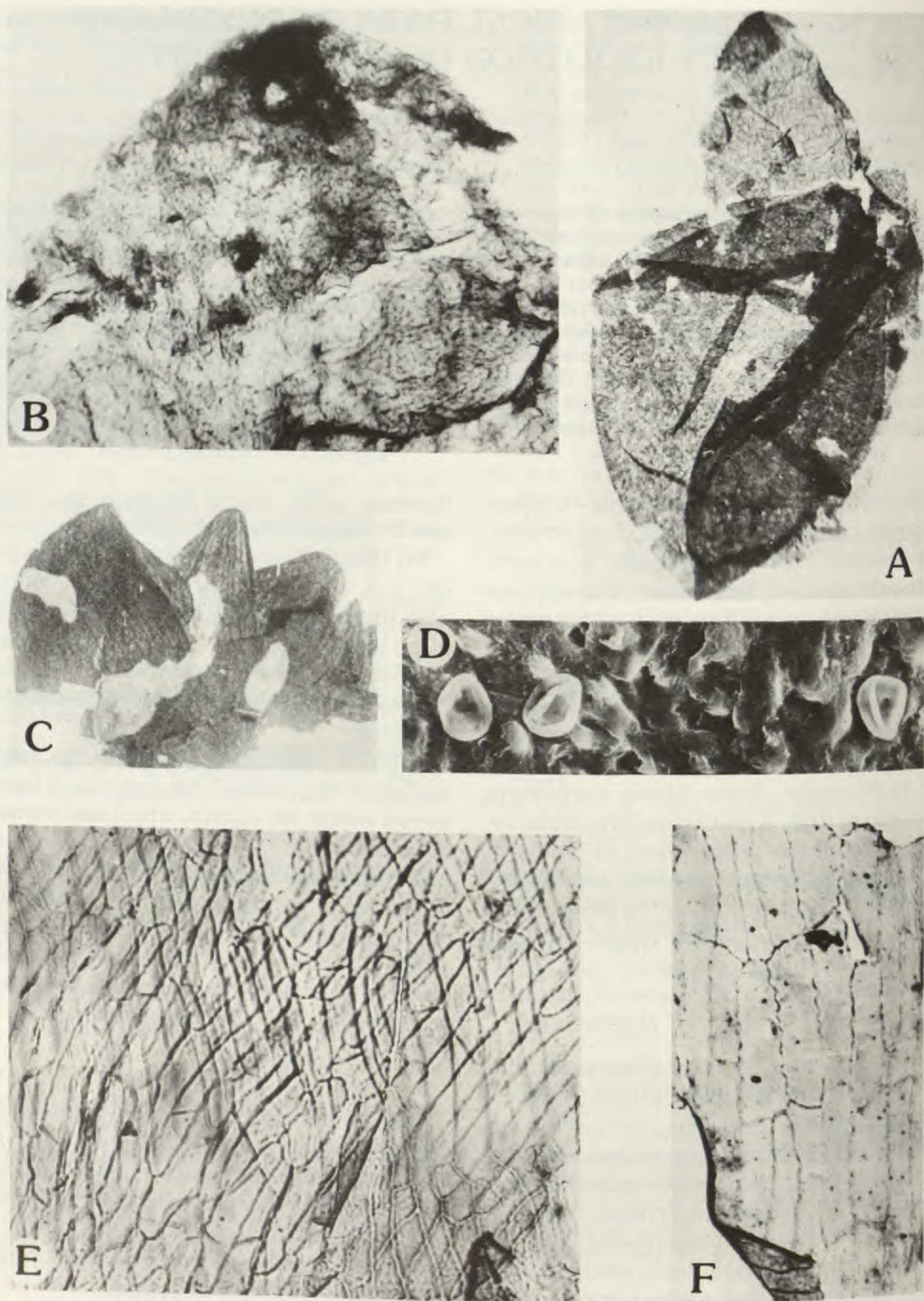


FIGURE 1. *Hirmerella* sp., lower Liassic of Odrovaz (Poland).—A. Two overlapping nucelli from an "ovuliferous scale" shown in C, 15 $\times$ .—B. Upper portion of a nucellus, 500 $\times$ .—C. "Ovuliferous scale," 5 $\times$ .—D. Scanning electron micrograph of pollen grains on the cuticle of a "scale," 500 $\times$ .—E. Joint cuticles of the locule and integument, 170 $\times$ .—F. Cuticle of the locule, 170 $\times$ .

rameev (in Vakhrameev & Kotova, 1977) as *Dicotylophyllum pusillum*.

In 1979, I visited this locality together with Dr. V. V. Zherikhin and other paleoentomolo-

gists with hopes of collecting more *Dicotylophyllum*. We failed to find it but instead concentrated on abundant enigmatic hirsute bodies previously brushed aside as insignificant "hairs."



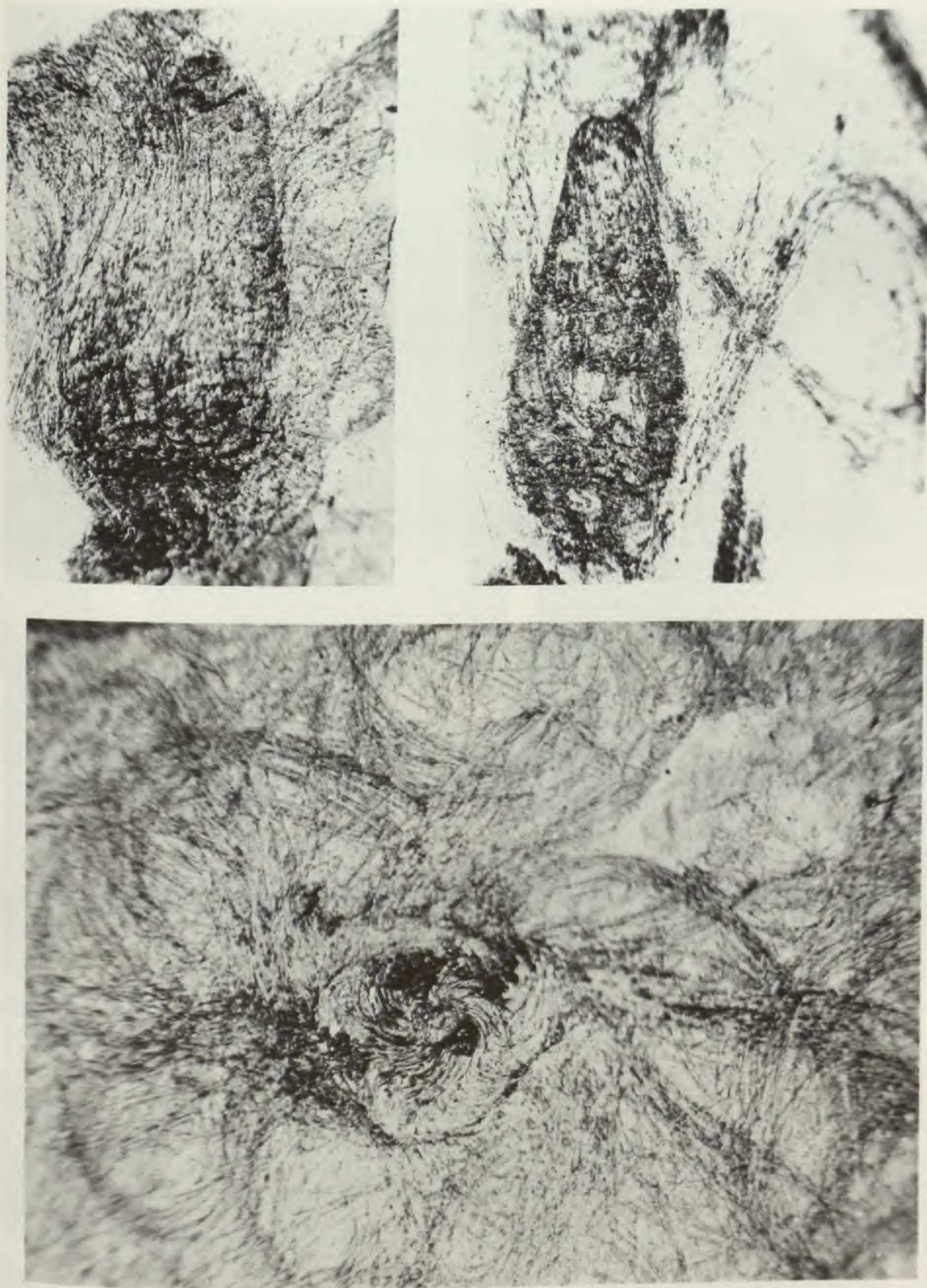


FIGURE 2. Achene-like fossils from the Lower Cretaceous of Baisa, Lake Baikal province. Two achenes showing epidermal cells, "coronas," and long hairs from the receptacles (top), 12 $\times$ , and a detached receptacle (bottom), 18 $\times$ .

These bodies were studied with a scanning electron microscope (SEM) and macerated. In effect they were shown to be achene-like diaspores, flask-shaped, with a persistent receptacle bearing long trusses of unicellular hairs (Fig. 2). Detached receptacles also occur abundantly on the bedding

planes (Fig. 2). The external coat ("cupule") shows large tubular epidermal cells arranged in longitudinal rows. These are clearly marked on impressions and can be seen under low magnification. The apical portion ("corona") is demarcated by a transverse groove and pitted. The



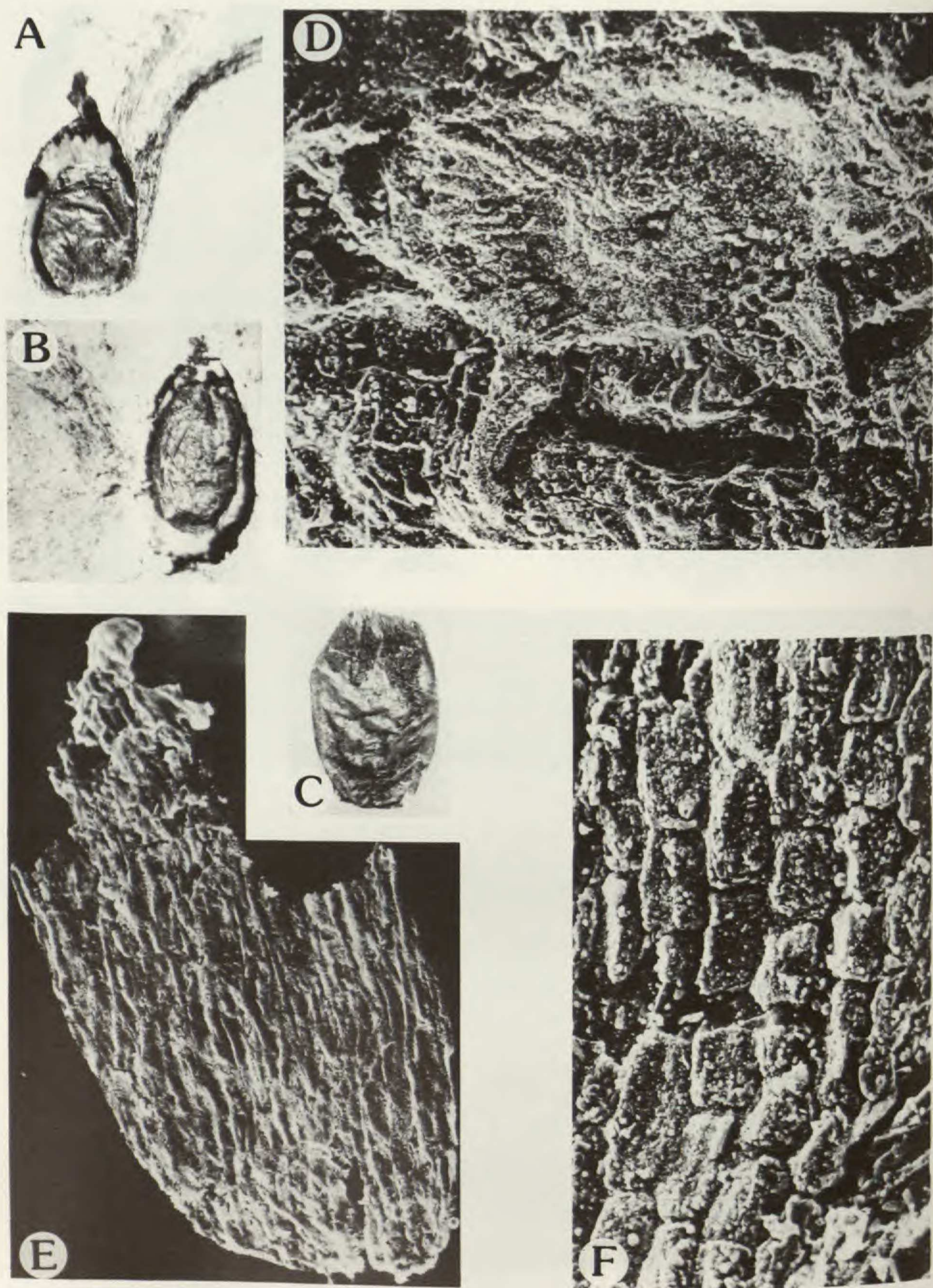


FIGURE 3. Achene-like fossils from the Lower Cretaceous of Baisa, Lake Baikal province. —A, B. Split achenes showing ovules,  $12\times$ . —C. Ovule from the achene shown in A,  $15\times$ . —D. Scanning electron micrograph of receptacle showing short bracts,  $140\times$ . —E. Scanning electron micrograph of nucellus with pollen grains at the top,  $60\times$ . —F. Scanning electron micrograph of epidermal cells,  $400\times$ .

receptacles show laminar appendages that appear mostly as short rounded lobes. In a favorably preserved specimen there are six small lanceolate bracts at the base (Fig. 3D). Hairs arise in fascicles from these appendages.

A few longitudinally split achenes have an inner cavity with a single ovule almost filling the locule. The ovules are elliptical, with an inconspicuous micropyle.

Externally, the cupules are scarcely cutinized



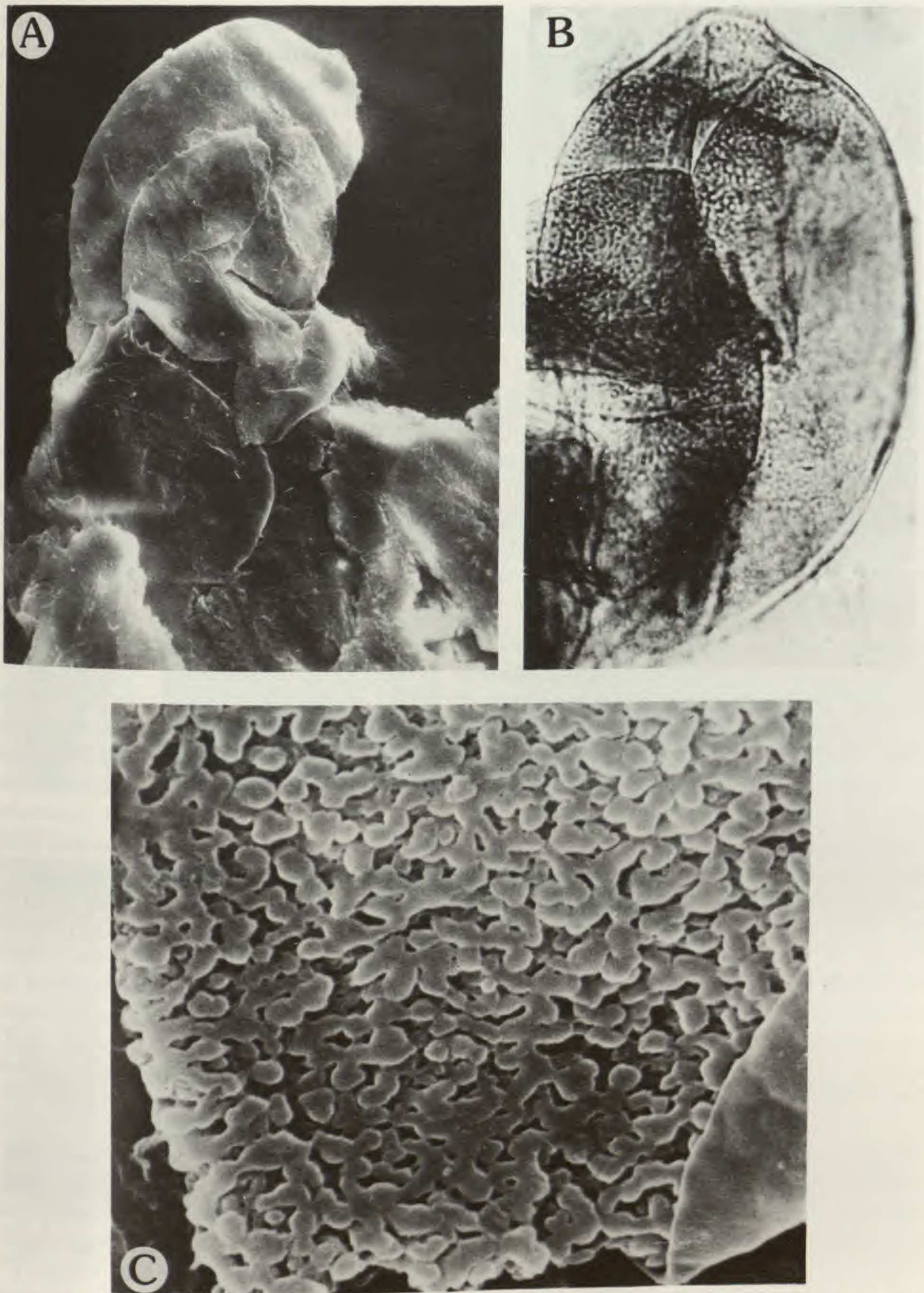


FIGURE 4. Achene-like fossils from the Lower Cretaceous of Baisa, Lake Baikal province.—A. Scanning electron micrograph of pollen grains on the top of a nucellus, same as in Figure 3E,  $400\times$ .—B. Top pollen grain showing sulcus,  $600\times$ .—C. Scanning electron micrograph showing infratectal clavate-rugulate pattern,  $10,000\times$ .

at all; at least I was unable to obtain an outer cuticle. The large-celled epidermis is underlain by a thin fibrous layer and much thicker stone tissue. Fragments of vascular bundles were macerated from the cupule wall. They consist of tra-

cheids with spiral thickenings. The ovules yielded two joint integumental cuticles and a nucellus that is thicker at the base but thin and unfortunately ill-preserved above. However, in one of the nucelli a cluster of pollen grains was observed



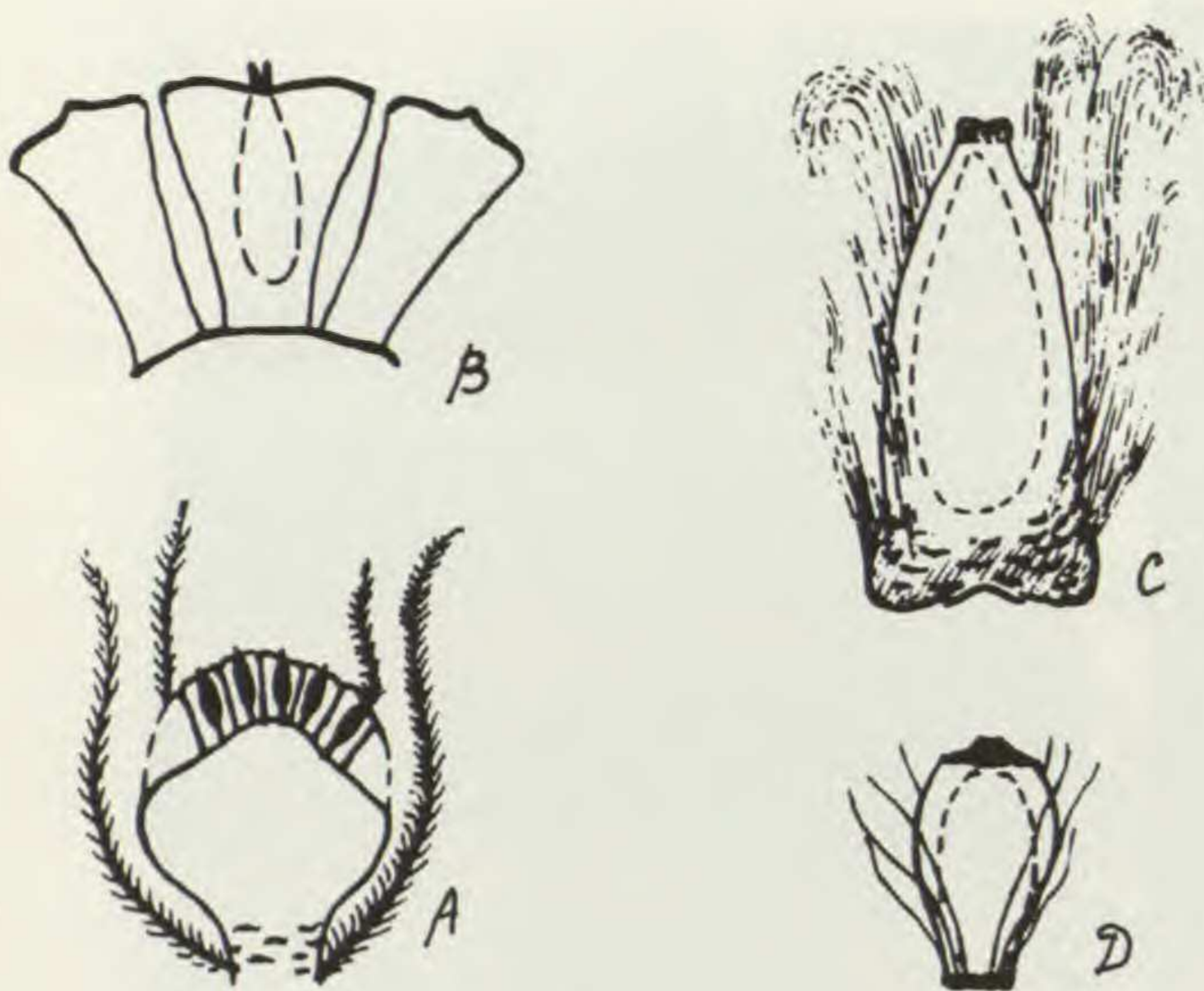


FIGURE 5. Suggested relationships of the Baisian achenes.—A. Bennettitalean flower with hairy bracts, ovules, and interseminal scales.—B. Bennettitalean interseminal scales fused around the ovule as in *Bennetticarpus crossospermum* Harris.—C. Baisian achene.—D. Cyperaceous achene (*Eleocharis* sp.).

at the apex (Fig. 4). They are elliptical, up to 140  $\mu\text{m}$  long, monosulcate, smooth, alveolar, showing clavate-rugulate infratectal structure at places where the tectum is dissolved (by some pollen chamber exudate?).

Superficially, these fossils look much like some cyperaceous achenes, especially those with abundant hypogynous hairs or bristles as in *Eriophorum* or *Carpha* (they might have been mistaken for such if met in geologically younger sediments). In *Eriophorum vaginatum* L., fascicles of bristles on a conical receptacle represent reduced perianth lobes. The shape and dimensions of the Baisian and *Eriophorum* achenes are much alike as well as the large tabular epidermal cells (Fig. 5).

The outer coat of a cyperaceous achene is currently interpreted as either a prophyll-derived membranaceous bladder (utricle) or a cupule formed by hypanthial growth of the receptacle (in *Scleriae*). Cupules of the Early Cretaceous Baisian achenes might have similar origin. However, on closer inspection they turned out to be neither cyperaceous nor even fully angiospermous because pollen grains occurred on the nucellus.

Among the Mesozoic plants, only bennettites stand for comparison. Their "flowers" have similar receptacles bearing perianth bracts that are often hairy. Reduction was a fashionable evolutionary mode in bennettites (Stidd, 1980). It is conceivable that the bracts were transformed into

vestigial outgrowths bearing fascicles of hairs. Similarly, numerous ovules might have been reduced to one while interseminal scales coalesced around it in a kind of a cupule. The clearly demarcated apical portions of the Baisian cupules are analogous to a "corona" of *Williamsonia* formed of the tips of interseminal scales. The nucelli and pollen grains are rather of bennettitalean aspect.

If these considerations were valid, then the Baisian plant could be seen as a development of certain bennettites toward proangiospermy. Whether they progressed further in the direction of monocots, as the similarity to cyperaceous achenes suggests, is an open question. An answer to this problem depends on further paleobotanical discoveries, as well as on new approaches to the cyperaceous morphology which, after so many efforts along conventional lines, is still in a mess.

#### ANGIOSPERMS AND ANGIOSPERM-LIKE FOSSILS FROM THE LOWER CRETACEOUS OF MONGOLIA

Lower Cretaceous lacustrine paper shales are widespread in Central Mongolia, Mongolian Altai, and Gobi. They were extensively studied by the Soviet-Mongolian paleontological expedition. On the evidence of fossil ostracodes, insects, fishes, and recently discovered abundant plant remains, these beds were assigned mostly to the Neocomian-Aptian. Fossil plant assemblages are dominated by conifers (*Brachyphyllum*, *Araucaria*, pinaceous seeds and seed scales) and ginkgophytes. In the Gurvan-Eren locality (western Mongolia), two species of winged angiosperm fruits were found (Krassilov, 1982). The larger fruit (Fig. 6B) has a spherical endocarp about 6 mm in diameter divided by a thick septa into two locules. The endocarp is embraced by a symmetrical membranaceous wing with reticulate venation and is crowned by a very short style bearing a funnel-shaped stigma. Comparison with superficially similar winged fruits, such as *Eucommia*, *Pterocaryopsis*, *Ptelea*, *Pteleacarpum*, *Zygophyllum*, *Dadonaea*, *Koelreuteria*, *Abronia*, *Dipteronia*, showed that this fossil fruit is hardly assignable to any of the known genera or families. There are, however, some points of resemblance with *Ptelea* and *Eucommia* provided that in the hypothetical ancestral species of the latter both locules were equally developed.

The smaller fruit (Fig. 6A) is elliptical, 2 mm long, having a short stalk and sessile stigma. The



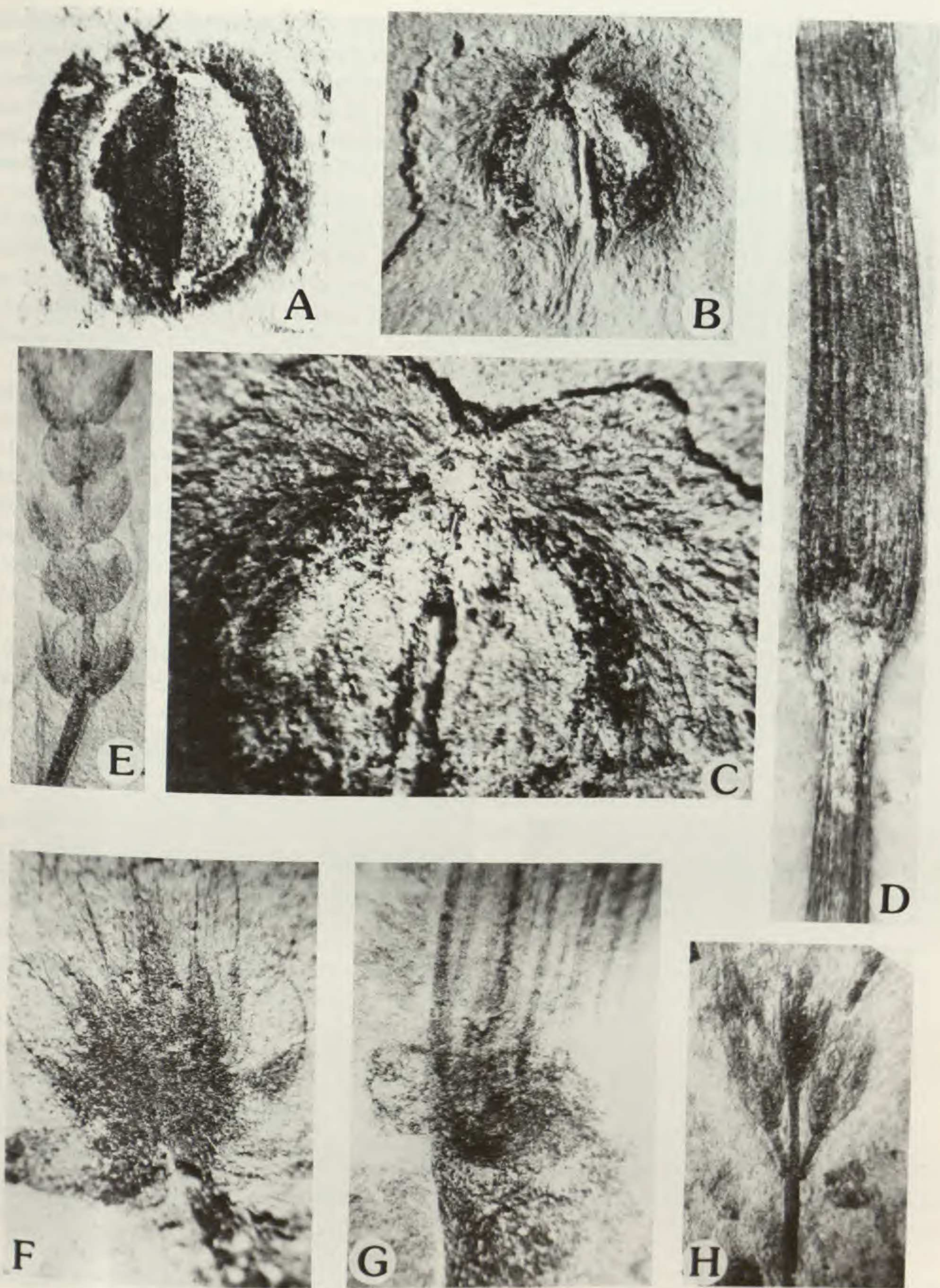


FIGURE 6. Angiosperm fruits and angiosperm-like fossils from the Lower Cretaceous of Mongolia.—A. Bilobulate fruit showing a smooth wing, 10 $\times$ .—B. Larger fruit showing a reticulate wing, 5 $\times$ .—C. Same as B showing a short style bearing a stigma, 10 $\times$ .—D. Grass-like leaf showing ligule, 2 $\times$ .—E. *Potamogeton*-like spike of five whorls of nutlets, 3 $\times$ .—F. *Sparganium*-like head of awned nutlets, 3 $\times$ .—G. Grass-like leaf showing auricle (left side of a sheath), 7 $\times$ .—H. Terminal inflorescence (?) of three spikes showing filamentous bracts, 3 $\times$ .



wing is narrow, smooth, and encircles the endocarp slightly obliquely to avoid the stalk, as in the winged fruits of Juglandaceae. Evolutionary significance of these findings is at present obscure but they widen the range of pre-Albian fruit diversity.

Another locality, Manlai in eastern Gobi, yielded fragments of articulate stems with sheathing leaves (Fig. 6D). The leaf blade is sessile, flat, having thick parallel veins and longitudinal striation. At the sheath-blade junction there is a conspicuous arched groove, probably representing a ligule. Short reflexed outgrowths are occasionally preserved at the sheath corners. They are comparable to auricles of bambusoid grasses. The general aspect of leaf blade and ligule is rather like in *Ancistrachne* and related southern hemisphere grasses.

There are also several kinds of what appear to be reproductive structures (Fig. 6F–H); (1) a cyme of three stalked spikes or spikelets, terminal on a stem, with three hair-like appendages (inflorescence bracts?) at the base, superficially resembling inflorescences of *Bulbostylis* and some other Cyperaceae; (2) *Potamogeton*-like spike with five whorls of three nutlets each; and (3) *Sparganium*-like fructification consisting of an axis bearing two sessile heads of about ten mucronate nutlets each, the lower one apparently in the axil of a leaf-like bract.

These fossils are approximately contemporaneous with the Baisian achenes. They may indicate initial diversification of marshy herbaceous monocotyledons or plants of the Baisian evolutionary level. Because they are not suitably preserved for detailed study, it is unsafe to draw any definite conclusions.

#### MIDDLE ALBIAN *CASPIOCARPUS*

*Caspiocarpus* from the western Kazakhstan is hitherto the most ancient structurally preserved fructification that proves the existence of true angiosperms in the late Early Cretaceous (Vakhrameev & Krassilov, 1979). Its age is determined rather rigorously as middle Albian (Vakhrameev, 1952). The fossil axis bearing two leaves and two paniculate reproductive structures was originally assigned to *Cissites* cf. *parvifolius* (Font.) Bell, the name being applied to the leaves (Vakhrameev, 1952). The details of panicles remained unknown until, in 1977, I was fortunate to obtain a few transfer and cuticular preparations revealing some essential characters. The

main axis is flat, grooved, 2 mm wide, branching at an acute angle. Each of the two branches bears a terminal panicle. One of them (the left one in Fig. 7A) is placed 5 mm above the leaf node. The panicles were shown to consist of two larger basal racemes and a number of much shorter crowded racemes above them. The latter are about 4 mm long bearing up to ten (mostly four or five), spirally arranged, overlapping follicles that are better seen in the loose apical portion of the right panicle (Fig. 7C). The follicles are elliptical, to 1 mm long, shortly beaked, attached by a short stalk and mostly opened.

It is seen on the casts and cleared preparations that they opened along the ventral suture and, in the upper quarter, also along the dorsal one (Fig. 8A). Their valves are mostly spreading at about 60° but sometimes they are flattened under pressure. No vestiges of stamens or perianths were found. The rounded pits on the casts of the follicles seen under SEM are hair bases or (less probably) stomata (Fig. 7F).

Several follicles contained intact ovules. In one of them, I found three ovules; two in one half of the follicle, one above the other (Fig. 8B), and a third one (Fig. 8C) juxtaposed to them. The ovules are about 0.8 mm by 0.5 mm, pointed, and broadly truncate at the hilar end. Two integuments are discernable, the inner one wedging out in the upper half (Fig. 8D) or occasionally near the middle of the ovule. The outer integument consists of two layers of tabular cells. Short unicellular hairs are scattered in the upper portion (Fig. 8D). The inner integument shows three layers of narrow spindle-shaped cells in the basal region. Some ovules are divided longitudinally into two halves (Fig. 8C). My suggestion that this feature represented a raphe in the cleared ovules was justly criticized by Retallack and Dilcher (1981), but at present I have no better explanation.

The taxonomic position of *Caspiocarpus* is uncertain. Because the seeds were retained in the dehiscent carpels, one can assume that they were attached by their funicles—a magnolialean feature. However, in the Magnoliaceae the carpels open along the ventral suture (with a single exception of *Kmeria*, see Canright, 1960). The thin-walled, ventrally dehiscent follicles are more characteristic of the Ranunculidae. In *Glaucidium*, an isolated genus related to Ranunculaceae and Berberidaceae, the follicles open at both ventral and dorsal sutures (Tamura, 1963).

The ovules are also of ranunculoid aspect, bi-



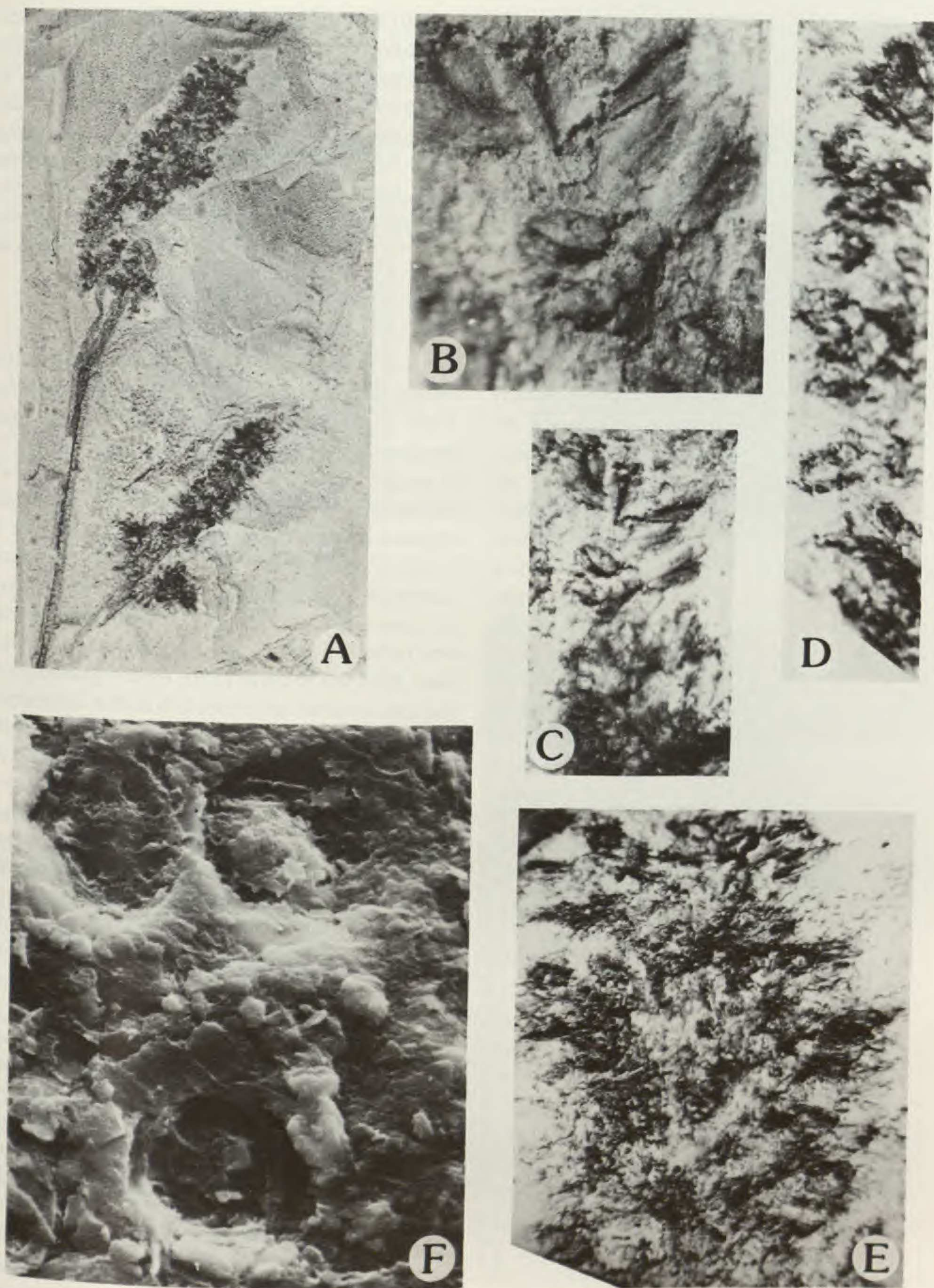


FIGURE 7. *Caspiocarpus* from the middle Albian of Kazakhstan.—A. Shoot bearing two leaves (light impressions inconspicuous on light matrix) and two panicles (1 = a leaf node), 2 $\times$ .—B, C. Apex of the right panicle showing loosely arranged follicles, 25 and 12 $\times$ .—D, F. Parts of the right panicle showing short lateral racemes with follicles, 10 $\times$ .—E. Scanning electron micrograph of pits (hair bases or stomata?) on the follicle, 2,000 $\times$ .

tegmic, with fairly thin integuments. In most Ranunculaceae the outer integument is typically shorter than the inner one, but the reverse relations occur in Berberidaceae, *Aquilegia*, *Hy-*

*drastis*, *Paeonia*, and some other genera within Ranunculidae. Extreme reduction of the outer integument is peculiar for *Ranunculus* and especially for *Circaeaster* where it is only two cells





FIGURE 8. *Caspiocarpus* from the middle Albian of Kazakhstan.—A. Small cleared follicle, dorsal view, 150 $\times$ .—B. Two ovules, 100 $\times$ .—C. Third ovule from the same follicle, 100 $\times$ . Portion of the same ovule showing wedging out of the inner integument and one of the integumental hairs, 150 $\times$ .



thick. Integumentary hairs are characteristic of *Helleborus*. Branching racemose inflorescences are known in *Aconitum* and *Cimicifuga*, but *Thalictrum* has panicles. Leaves of *Cissites* morphotype occur in such extant Ranunculaceae as *Delphinium*, *Aconitum*, and *Ranunculus*. I believe, therefore, that *Caspiocarpus* was most closely related to Ranunculidae, though possibly not assignable to any existing family.

#### DISCUSSION

Hickey and Doyle (1977) have stated that "the identification of any Jurassic plants as proangiosperms (as attempted by Krassilov, 1973, 1975) will probably be a difficult task requiring a detailed comparative analysis of all organs as rigorous as that which was required to establish the relationship between cordaites and conifers (Florin, 1971) or the role of Devonian Aneurophytales and Archaeopteridales as progymnosperms." Needless to say, the rigorous analysis of all organs is desirable, but Florin actually drew his conclusions from his studies of the seed scale complexes—which did prove the relationship between cordaites and lebachiacean plants (probably a specialized line of cordaites with reduced leaves), but which left the problem of conifer ancestry unsolved. Evidence that progymnosperms are related to gymnosperms comes mostly from wood anatomy.

Similarly, the proangiosperms, as I understand them, share with true angiosperms a few characters of critical importance, and among them the angiospermy itself. They have a kind of ovary that is supposedly monocarpellate involuted (*Caytonia*, *Dirhopalostachys*) or bicarpellate with open carpels (*Leptostrobus*). The question is whether any kind of angiospermous ovary could arise from these structures or whether they represented "blind alleys" of angiospermization while the mainstream progenitors are still to be found.

Thomas (1931) has suggested derivation of a ranunculoid follicle from two joined caytonian cupules fused to the rachis. His ideas were rejected by leading contemporaneous morphologists because in *Caytonia* the ovules are orthotropous and supposedly unitegmic whereas in ranunculoid angiosperms they are mostly bitegmic and anatropous. To overcome the difficulty of a de novo formation of the second integument, Gaussen (1946) has postulated its derivation from the caytonian cupule while

the rachis expanded into a carpel. Stebbins (1974) and Doyle (1978) have supported this suggestion but Retallack and Dilcher (1981) found it intuitively unattractive. In their opinion, the outer integument might have been derived from a glossopteridalean leaf bearing an epiphyllous ovulate structure. But in the case of *Caytonia* there is no need of going to those lengths because its ovules are, in fact, bitegmic.

I suggested (Krassilov, 1970) that the enigmatic "spotted layer" of *Caytonia* (supposedly an aleurone layer) might be a vestigial inner integument. Recently I studied a few *Caytonia* ovules from Yorkshire kindly sent to me by T. M. Harris. I found nothing essentially new except some fine external features of the micropyle (Fig. 9). I also reaffirmed my suspicions about the "spotted layer." The aleurone layer is a layer of endosperm. It is situated inside, not outside the nucellar cuticle. The "spotted layer" of *Caytonia* envelopes the nucellus (Fig. 10). It consists of two layers of cells and it is cutinized. Its small spots and larger patches of dark matter look not like aleurone grains but rather like metamorphosed oil cells and blocks of tannin filling inner integuments of angiosperm seeds. Harris (1964) noticed that the "spotted layer" never extended into the micropyle. Thus, the micropyle was formed by the outer integument only. I discussed the problem of bitegmy elsewhere (Krassilov, 1970). Double integuments can be traced back to early Carboniferous *Eurystoma angulare* (Camp & Hubbard, 1963). In many Paleozoic seeds the inner integument had been lost in fusion with the nucellus (hence, vascularized nucelli), but it was restored in gnetalean plants, some bennettites (*Vardekloeftia*, Harris, 1932), and *Caytonia*. About half of the dicotyledons and three quarters of monocotyledons have bitegmic ovules that are consentaneously recognized as the primitive condition. However, in the families that appeared early in the fossil record, such as Ranunculaceae, Menispermaceae, Piperaceae, Fabaceae, Rosaceae, and Poaceae, there are both uni- and bitegmic ovules. Such flexibility might be due to frequent atavistic mutations. Even vascularized nucelli have been restored in some angiosperm lineages (e.g., Thymeliaceae). Trittegmic forms, as in *Sarcandra*, can also be expected among early angiosperms.

It was shown (Krassilov, 1978) that the "mouth" of *Caytonia* can be shifted from its position at the base of the pedicel. One can imagine that a continuation of this process (due to



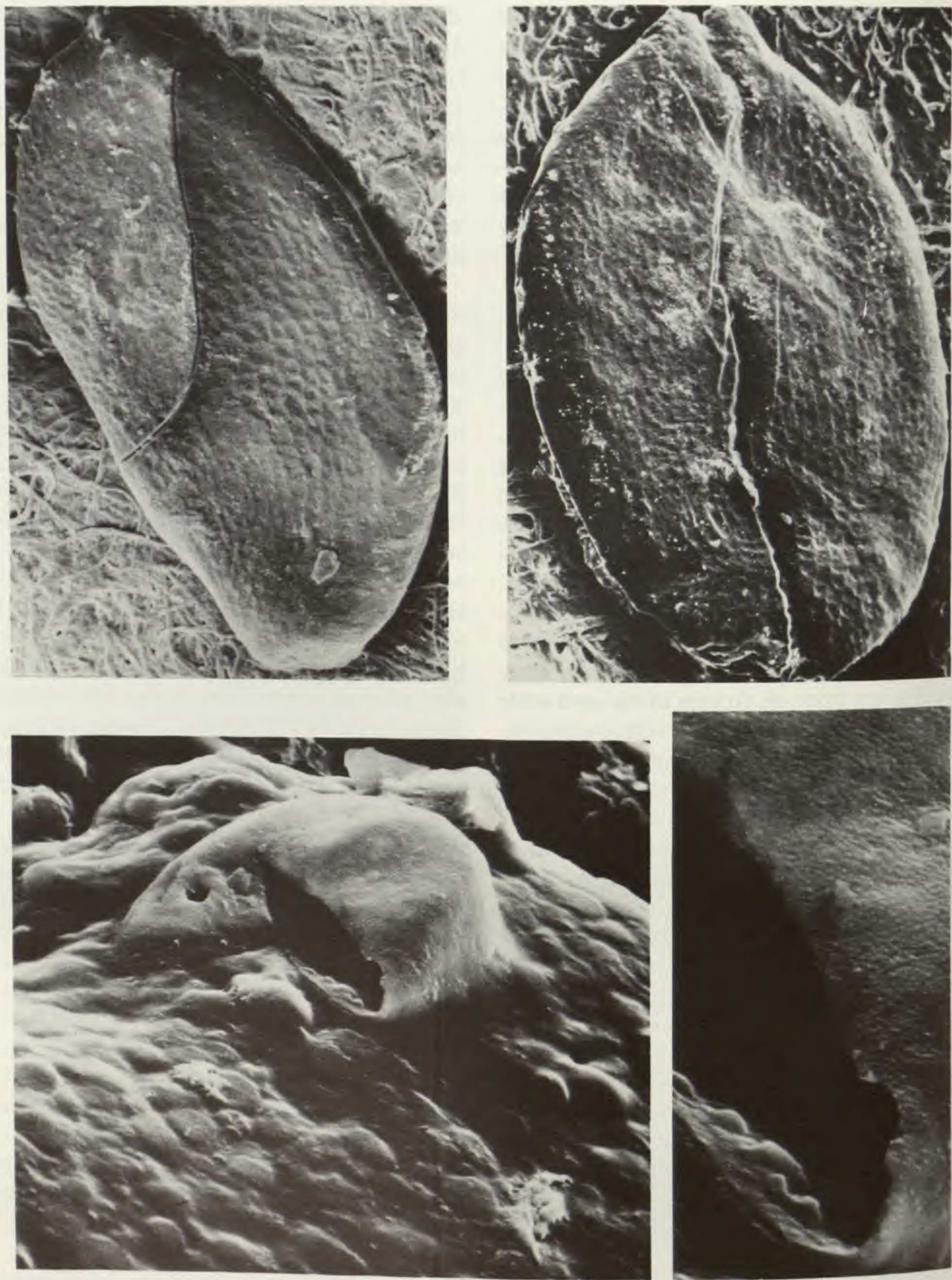


FIGURE 9. *Caytonia sewardii* Thomas from the Jurassic of Yorkshire. Scanning electron micrograph of two ovules,  $100\times$ , and scanning electron micrograph of details of the micropyle of the left ovule,  $1,200$  and  $4,000\times$ .

adaptation to some pollination vector?) could bring the "mouth" into apical position, at the same time affecting the position of ovules. The resultant urn-shaped ovary, styleless, with sessile stigma, would not be unlike those of a vesselless angiosperm, *Sarcandra irvingbailleyi* Swamy (Fig. 11). In this species, the ovules are bitegmic (oc-

asionally tritegmic), orthotropous but brought to pseudoanatropous position by the curvature of the carpel (Vijayaraghavan, 1964). Intercarpellary pollen grains, as in *Caytonia* (Krassilov, 1977b) occur as an atavistic or recurrent feature in *Annona*, *Lilium*, and some other angiosperms (Vasil & Johri, 1964).



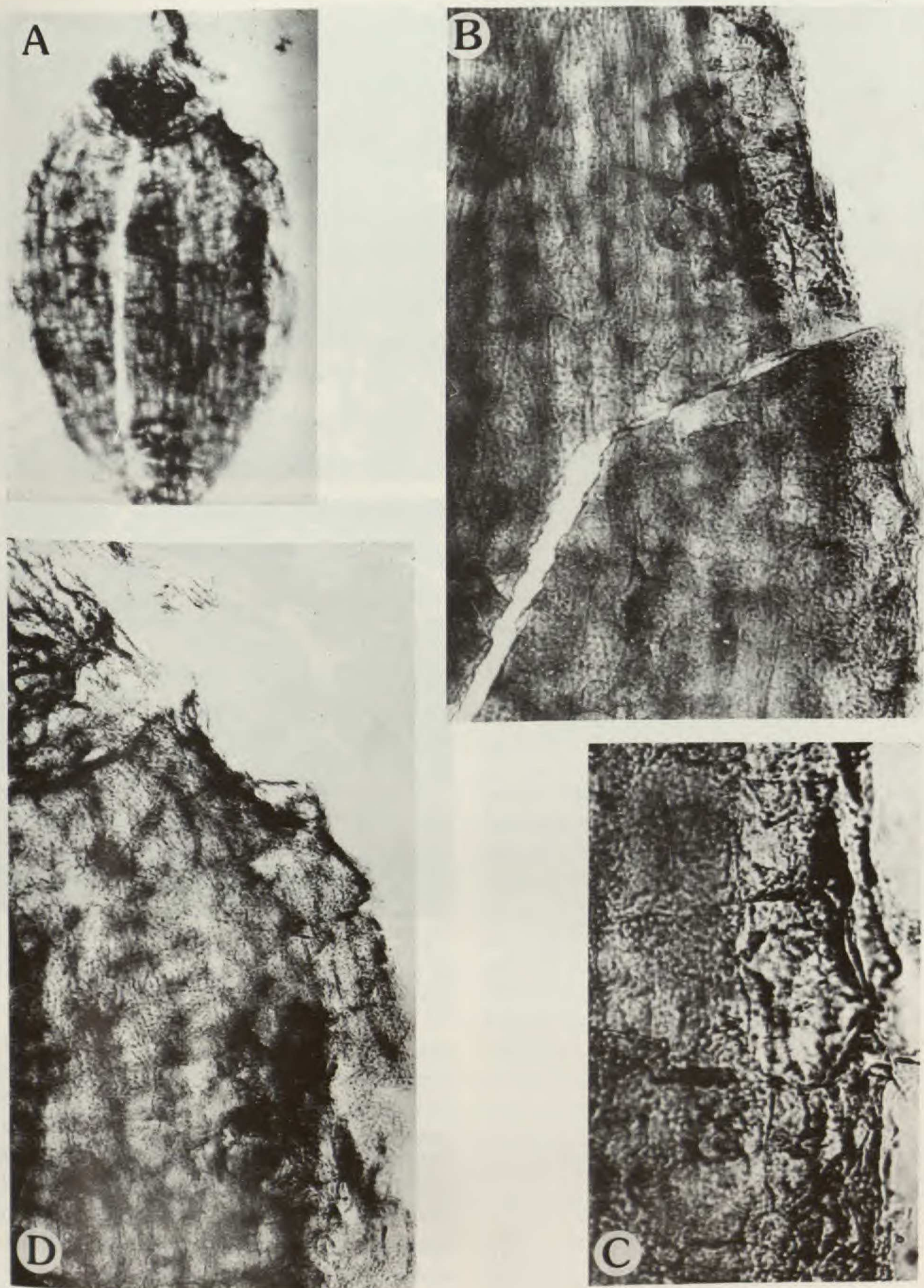


FIGURE 10. *Caytonia seawardii* Thomas from the Jurassic of Yorkshire.—A. Nucellus of an ovule shown in Figure 9, right, with the remnants of a "spotted layer," outer integument is removed completely,  $70\times$ .—B. "Spotted layer" of another ovule,  $150\times$ .—C. Cells of the "spotted layer,"  $300\times$ .—D. "Spotted layer" wedging out below the micropyle,  $150\times$ .



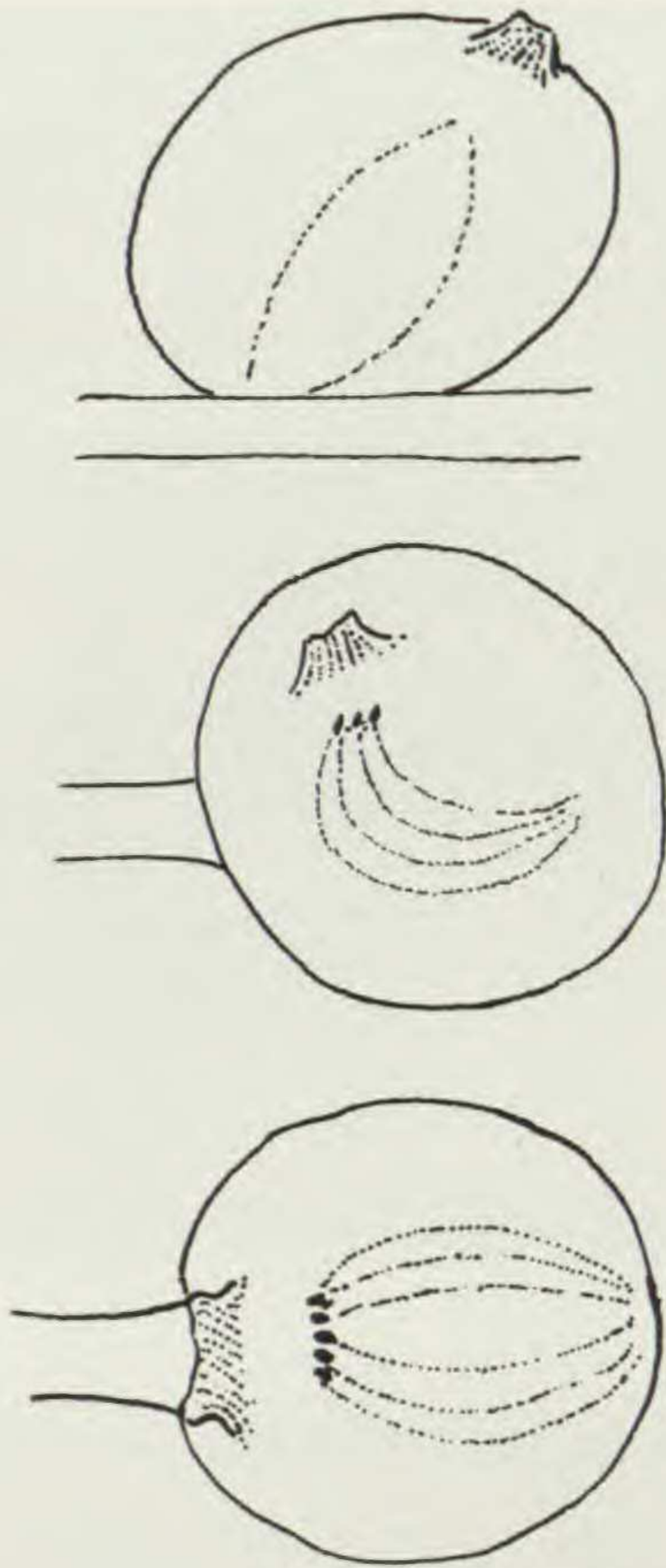


FIGURE 11. Suggested derivation of a *Sarcandra*-like carpel from *Caytonia*-like cupule by the shifting of a mouth.

This simple mode of transforming the caytonian cupule into a carpel is partially supported by the evidence of the shifted "mouth" in the mid-Jurassic *Caytonia sewardii*, but final proof or repudiation should come from detailed study of the late Jurassic and Cretaceous species.

*Dirhopalostachys* is a raceme of paired follicle-like one-seeded beaked cupules having a ventral suture (Krassilov, 1975). The pairing of cupules reminds one of the Hamamelidaceae—one of the

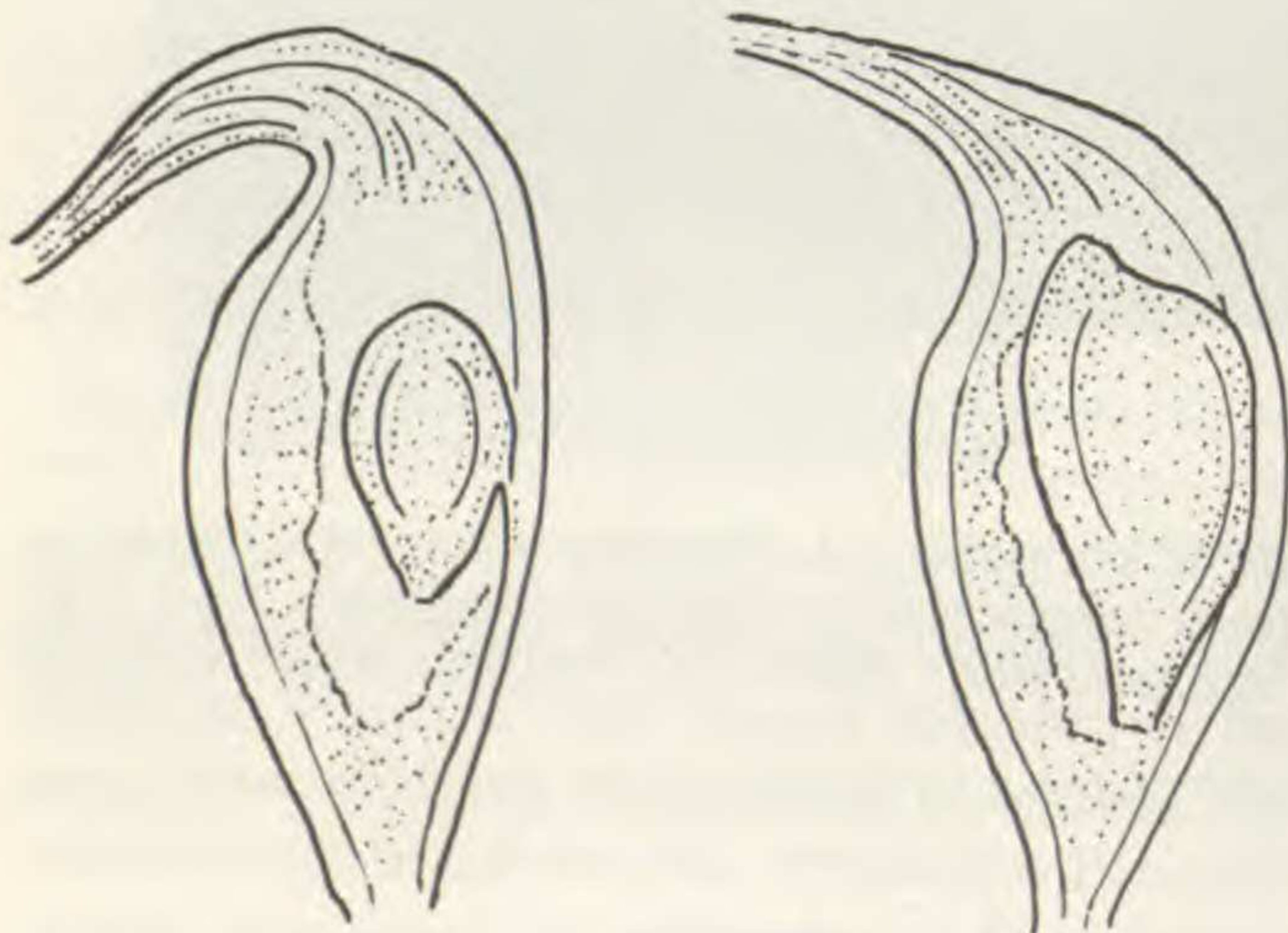


FIGURE 12. Carpels of *Kingdonia*, left (after Foster, 1961) and *Dirhopalostachys* (after Krassilov, 1975).

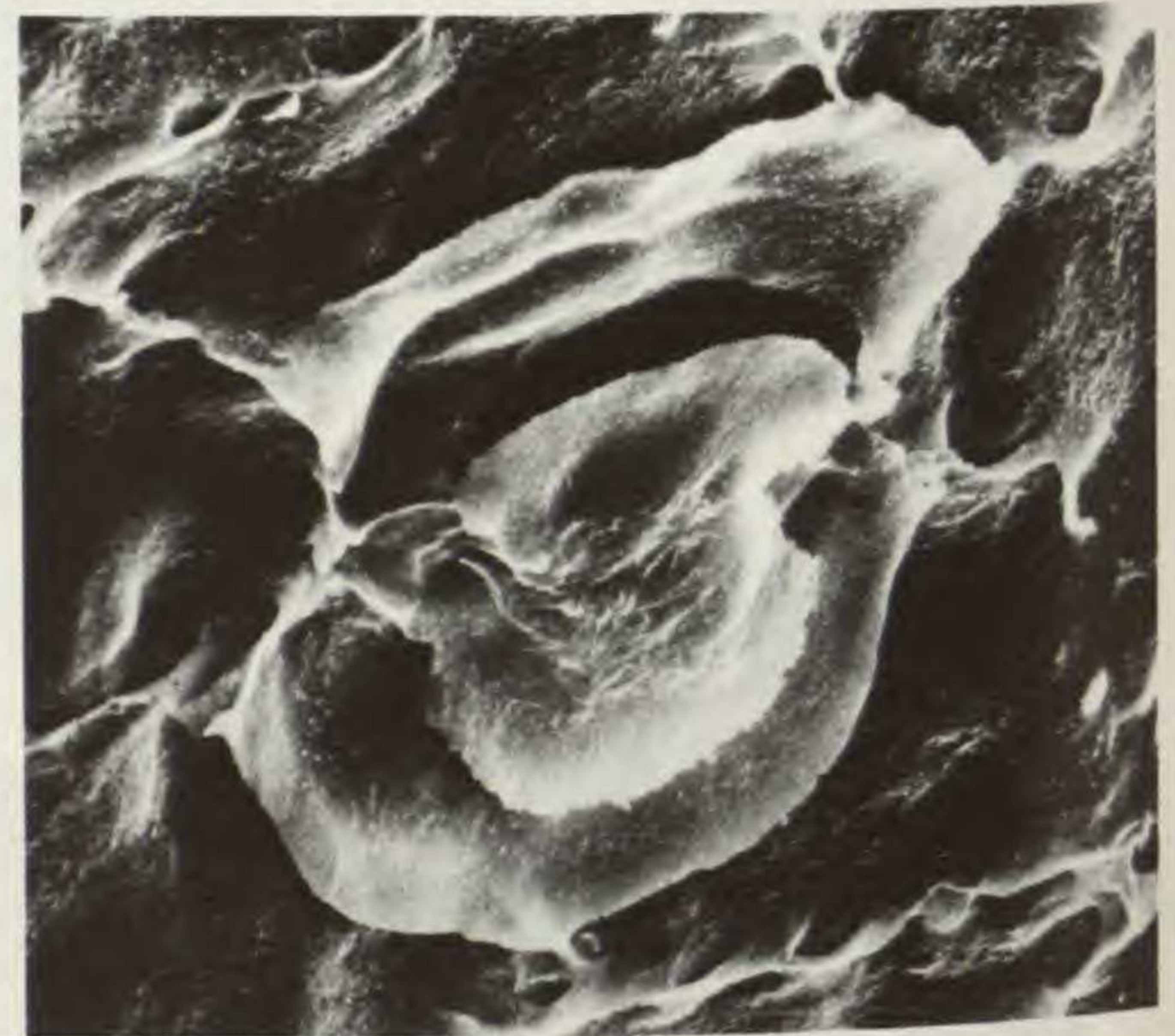
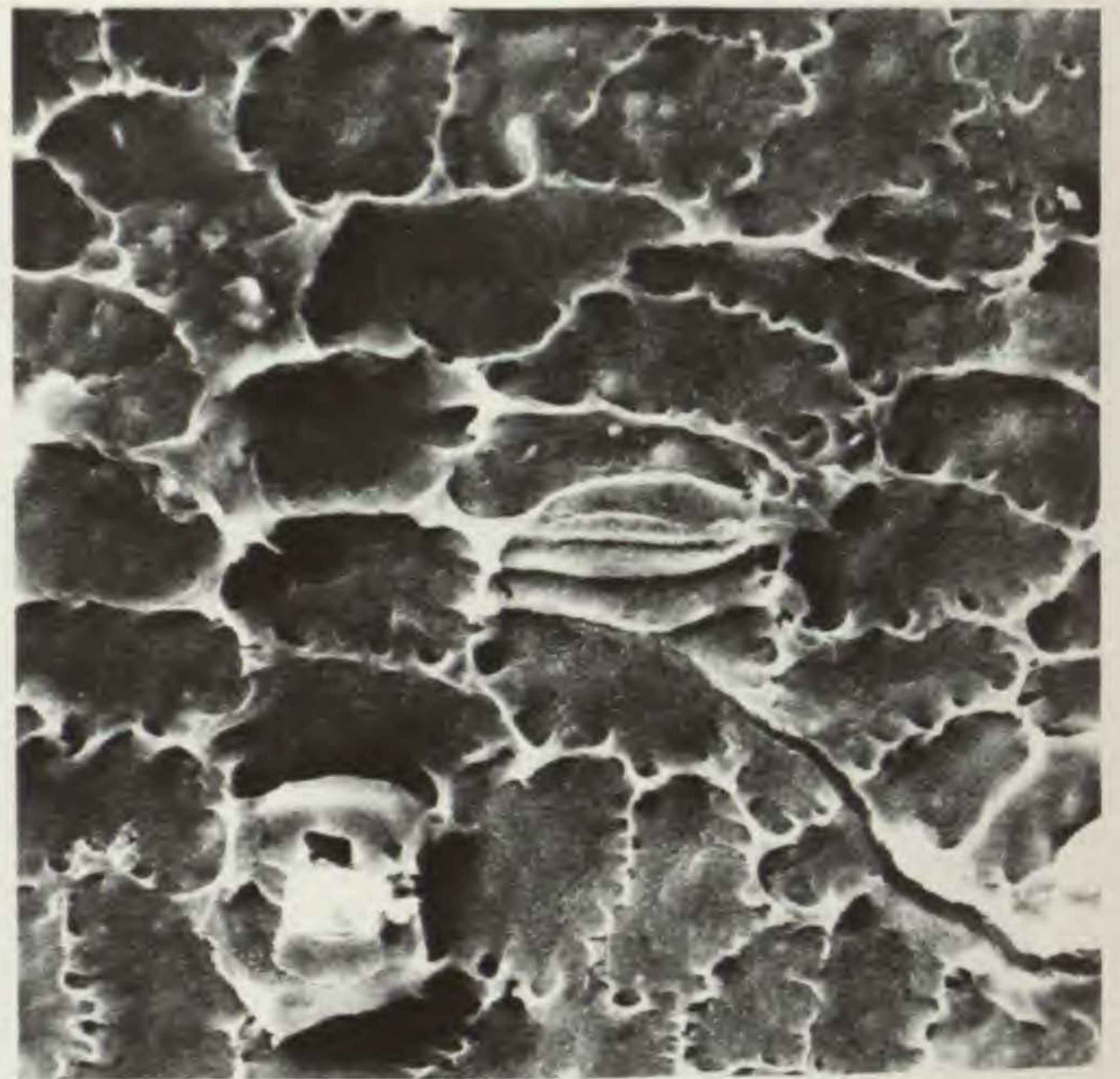


FIGURE 13. Scanning electron micrograph of aborted (top) and normal stomata of a bennettite *Nilssoniopteris amurensis*, 800 and 1,600 $\times$ .

most ancient angiosperm families. However, the cupules are even more similar to the carpels of *Kingdonia* (Foster, 1961). In this archaic east-Asiatic genus, the gynoecium consists of 5–8 spirally arranged semiclosed carpels that develop into one-seeded fruits with recurved beaks (Fig. 12). Noticeably, the venation in *Kingdonia* is open flabellate in leaves and open pinnate in tepals, resembling *Nilssonia*—supposed foliage leaves of *Dirhopalostachys*. It is conceivable that the apetalous flower of *Kingdonia* arose from androgynous reproductive structure similar to *Irania*—a progymnospermous plant related to *Dirhopalostachys* (Schweitzer, 1977). *Kingdonia* certainly deserves further study. However, many essential features of *Dirhopalostachys* and *Irania*, and first of all the mode of pollination, are still to be learned.





FIGURE 14. Vessel-like members from the midrib of a *bennettitalean* (*Otozamites*) pinna showing terminal perforations, 300 and 600 $\times$ .

Paleobotanical discoveries have substantiated almost all theoretically conceivable pathways from open ovulate structure to carpel except conduplication. In the course of my studies of the Late Jurassic *Leptostrobus* (bivalvate capsules with papillate stigmatic fringes), I suggested that the so-called "conduplicate" carpel in Winteraceae is derivable from the leptostrobalean prototype and actually consists of two open carpels fused by their margins (Krassilov, 1970). The conduplicate nature of the winteraceous carpel was questioned by Tucker and Gifford (1964) and recently Leroy (1977) has shown that, at least in some winteraceous genera, the ovary is bicarpellate, with both ventral and dorsal grooves corresponding to the contacts of open carpels as it was, in fact, suggested by me and still earlier, on different grounds, by Long (1966). Vink (1978) noted that in the supposedly unicarpellate ovary of *Drimys*, the dorsal groove is identical to that of the bicarpellate ovaries studied by Leroy. Complete revision of the carpel morphology in Winteraceae, one of the key families of angiosperm phylogeny, is to be expected.

Finally, if the supposed relationships of the Baisian achenes to ovulate structures of bennettites were correct, there should be still another way to angiospermy by fusion of interseminal scales, vaguely preconceived by Fagerlind (1946).

Evolutionary potentials of bennettites look not so gloomy once more. Recently other points of resemblance between them and angiosperms came to light. Florin (1933) suggested that bennettitalean stomata were mesogenous ("syndetocheilic") as in many angiosperms, but his views were disputed because he deduced from mature paracytic apparatuses, which can be ontogenetically mesogenous, perigenous, or mesoperige-

nous. Recently, I described a few aborted stomata (Fig. 13) that confirm mesogenous development (Krassilov, 1978). In the Mongolian species *Otozamites lacustris* Krassil, it was possible to macerate conducting elements from the midrib of a pinna (Krassilov, 1982). Among the tracheids with scalariform thickenings, there were short vessel-like members showing terminal perforations (Fig. 14).

Thus, bennettites were capable of developing vessels in the primary xylem, reticulate venation (*Dictyozamites*), paracytic stomata, bisexual flowers, and achene-like fruits. It seems unjust to rule them out as possible ancestors of angiosperms. There are also indications that angiosperms first appeared in cycadophyte shrublands dominated by various bennettites and then penetrated coniferous forests (Krassilov, 1973).

#### CONCLUSION

Not long ago, the origin of angiosperms seemed mysterious because there were no acceptable candidates for ancestors. Now the problem is that there are too many of them.

Traditionalists often pose as defenders of respectable theories (such as monophyletic origin of angiosperms) against irresponsible speculations. Actually, they defend old irresponsible speculations from the new ones. In the case of angiosperm ancestry, however, new speculations even seem somewhat less irresponsible. As more lineages approaching angiospermy emerge from the fossil record, the polyphyletic hypothesis appears more plausible. It is significant also that most proangiosperm records are clustered around the supposed Asiatic center of origin.

Further progress depends on detailed studies of the Late Jurassic and early Cretaceous *Caytonia*, *Dirhopalostachys*, bennettites, czeckanowskian, and *Classopollis*-producing plants as well as the middle Cretaceous angiosperms.

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